New records of distribution and nesting of two species of Cypseloidine swifts in western Panama, with notes on additional species

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SUMMARY.—We searched for nesting Cypseloidine swifts at 22 waterfalls in western Panama during April 2013 and April–August 2014. Three nests of Spot-fronted Swift *Cypseloides cherriei* were found, providing the first record of occurrence in Panama. White-chinned Swift *C. cryptus* was found at five sites, which is the first report of nesting in Panama. Chestnut-collared Swift *Streptoprocne rutila* nests were found at three waterfalls. White-collared Swift *S. zonaris* was found nesting at two sites and a roost site was found at a third waterfall. Nesting phenology and nest elevations are discussed. Field identification marks for *C. cryptus* are reviewed.

Scant information and few reliable sight records exist for swifts of the genus *Cypseloides* in Panama. This is due in large part to the difficulty of identifying swifts in flight and their habit of nesting in hard-to-see locations at waterfalls. In North America, regional searches have been undertaken for nesting Black Swifts *Cypseloides uiger* (Knorr 1961, Foerster & Collins 1990, Levad *et al.* 2008, Horvath 2012). The primary reference for Cypseloidine swift nesting data in Central America is the detailed study by Marín & Stiles (1992) at one site in Costa Rica.

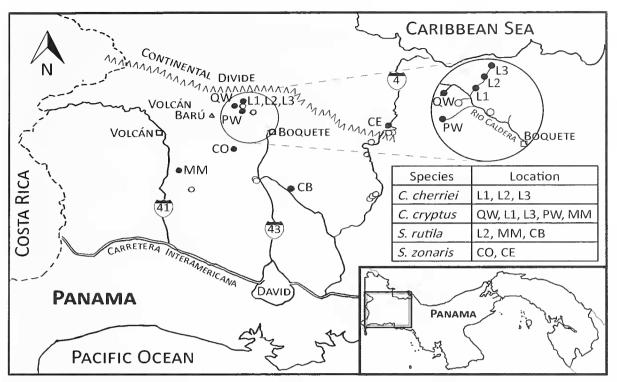
This paper presents data from a widespread survey of waterfalls in western Panama that provide new records of distribution and nesting details for Spot-fronted Swift *Cypseloides cherriei*, White-chinned Swift *C. cryptus*, Chestnut-collared Swift *Streptoprocue rntila* and White-collared Swift *S. zonaris*.

Methods

In April 2013 and from April until August 2014 we searched for nesting Cypseloidine swifts at 22 permanent, year-round waterfalls in western Panama (Fig. 1) by carefully scanning wet rock faces around and behind waterfalls using binoculars and telescopes. The precise locations of the study sites are presented in the legend to Fig. 1. Nearly all searches were conducted in the middle of the day when sunlight provided bright conditions for observation. At six sites where nests were found, we returned on subsequent days to conduct follow-up observations; on some visits, misty conditions prevented us from determining nest contents.

At all but two nesting sites, we observed from a distance to avoid flushing or otherwise disturbing the birds. We observed only from eye level and did not climb to nests or use a mirror on a pole to inspect nest contents, so in most cases we were unable to determine if the adult on the nest was incubating eggs or brooding young. At site QW an adult swift was mist-netted, measured and released. Measurements were taken using a metal wing rule and callipers following standard parameters (Pyle 1997). An infrared camera was set up to record activity for 72 consecutive hours at the same site.

We conducted five evening watches at waterfalls following the methodology of Levad *et al.* (2008) which was developed for surveying Black Swift nests in the USA. However, because our study area is within the range of three swift species with similar



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Figure 1. Map of survey sites in western Panama: black dots = occupied waterfalls, open circles = unoccupied sites. Location of the sites: L1 = $08^{\circ}50'30''N$, $82^{\circ}28'35''W$; L2 = $08^{\circ}50'35''N$, $82^{\circ}28'26''W$; L3 = $08^{\circ}50'41''N$, $82^{\circ}28'19''W$; MM = $08^{\circ}41'06''N$, $82^{\circ}36'23''W$; CO = $08^{\circ}44'02''N$, $82^{\circ}29'56''W$; CE = $08^{\circ}47'07''N$, $82^{\circ}11'16''W$; QF = $08^{\circ}50'49''N$, $82^{\circ}29'24''W$; PW = $08^{\circ}49'01''N$, $82^{\circ}29'35''W$; CB = $08^{\circ}38'55''N$, $82^{\circ}23'45''W$.

flight silhouettes (Spot-fronted Swift, White-chinned Swift, Chestnut-collared Swift), we determined that the evening watch was not a useful survey technique in Panama because low light conditions prevented accurate species identification as they flew to roost.

Results

We found swifts nesting at nine of 22 waterfalls surveyed; the remaining 13 waterfalls appeared to be unoccupied. We cannot eliminate the possibility of nesting at the unoccupied waterfalls, since many were surveyed only once. However, most of these 13 waterfalls lacked either potential nest platforms that would be inaccessible to ground predators or the cliff overhangs necessary to protect nests from inclement weather.

SPOT-FRONTED SWIFT Cypseloides cherriei

Three nests were found, each at a different waterfall along the same tributary of the Caldera River in an area of steep slopes and primary montane forest, at elevations of 1,745 m, 1,830 m and 1,945 m (Fig. 1: sites L1, L2, L3). Horizontal distance between waterfalls was *c*.300 m. The nests were located on vertical cliff faces 10 m, 8 m and 7 m above the base of the falls, which had approximate heights of 25 m, 15 m and 15 m, respectively. Each nest was in the zone of continuous mist within 3 m of the 'curtain' of falling water, in a dark location but unobscured by vegetation, protected from above by a rock overhang, and rarely received direct sunlight. We observed a torrential rainfall event in June 2014 when the creek flooded, but at each nest the rock roof prevented the nest from washing away. Two nests were on ledges (Figs. 2–3) and one was in a 'pocket'; in each case, the swifts entered and left the nest by direct flight from the nest rim.

Despite searching flocks of swifts in flight, we only observed Spot-fronted Swifts on the nest or flying directly along the canyon to the nest; we saw none in flight away from their

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Figure 2. Adult Spot-fronted Swift *Cypseloides cherriei* incubating or brooding, site L3, western Panama, 13 June 2014 (Eric G. Horvath)



Figure 3. Spot-fronted Swift Cypseloides cherriei incubating, site L2, western Panama, 15 May 2014 (Lloyd Cripe)

nesting waterfalls. We were able to track the success of these three nests and each appeared to successfully fledge one young. Our observations have enabled us to create an outline of nesting phenology for 2014: egg laying in May, hatching in June, and fledging in late July to August.

WHITE-CHINNED SWIFT Cypseloides cryptus

Five occupied sites were found at elevations of 880 m, 1,745 m, 1,840 m, 1,945 m and 1,980 m; each was at a separate waterfall and had just one pair of swifts nesting (Fig. 1: sites MM,

L1, QW, L3, PW). One nest was easily visible while the others were partially concealed behind ferns and other vegetation; all were in wet areas beside or under falling water (Figs. 5–7).

The nest at site L3 was monitored regularly throughout the nesting season. An adult was first observed incubating on 5 May 2014, and the first observation of a chick in the nest was on 13 June. The developing chick was viewed in the nest until 28 July when it appeared large, healthy and was flapping its wings. It was absent on our next visit on 7 August.

At site QW on 11 June 2014 an adult White-chinned Swift was trapped (Fig. 4)



Figure 4. White-chinned Swift *Cypseloides cryptus*, site QW, western Panama, 11 June 2014 (Eric G. Horvath)



Figure 5. Adult White-chinned Swift *Cypseloides cryptus* incubating, site L3, western Panama, 15 May 2014 (Lloyd Cripe)

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and measured: flattened wing 132 mm, tail 43 mm, exposed culmen 5.4 mm. Wing moult was underway, with pp1–3 new and fully grown, pp4–5 in sheath and partially grown, and the outer pp6–10 old and worn. The tail was worn with frayed tips; no exposed rachis was present on any of the rectrices.

The infrared camera placed adjacent to the nest at site QW took one photo every five minutes and whenever motion was detected, resulting in 1,160 photos during the period 18–21 June 2014. On 18 June 2014 the single chick in the nest was covered in dark grey semi-plumes (Collins 1963) and gave a raised-wing threat display. It was estimated to be 15–20 days old. The chick had a skin temperature of 30°C, measured using an infrared thermometer 10 cm away; the chick's core temperature was probably higher. Ambient temperatures 1 m from the nest varied at 12–17° C. The photo sequence enabled us to document the following nest activity. The chick was brooded near-continuously by one adult at night, while the other adult roosted 1 m from the nest. Nest change-overs occurred during the night, and at times two adults were present at the nest simultaneously with the chick. Apparent nocturnal provisioning of the chick was visible in some photos. By day, the adults were largely absent, especially in the morning, when the chick was alone and did not exhibit torpor.

CHESTNUT-COLLARED SWIFT Streptoprocne rutila

We found three nests at geographically widely separated waterfalls at elevations of 350 m, 880 m and 1,830 m (Fig. 1: sites CB, MM, L2). Two nests were on cliffs next to waterfalls in somewhat drier locations than the *Cypseloides* nests and the third nest was at the back of an 8 m-deep cave located at the base of a waterfall. The cave nest, site L2, was observed during construction in mid April, and the first egg was noted on 15 May. A second egg was seen on 20 May, but by 22 June the nest had collapsed. We suspect that the nest was disturbed by humans, as it was in an easily accessible location on a popular hiking trail. The swifts started rebuilding the nest in July, later in the rainy season, but did not lay a second clutch. The other two nests were not regularly monitored, so we lack data on nest success.

WHITE-COLLARED SWIFT Streptoprocne zonaris

We observed one nest of this species at site CO (1,350 m elevation, Fig. 1) on 12 June 2014. The nest held two large, well-feathered young and a single adult. There was also a large colony of White-collared Swifts nesting at site CE, at 600 m elevation. Here *c*.100 adults were observed flying to and from their nests at midday on 16 June 2014, but we were unable to see and therefore count the nests due to access difficulties. At Cañon Macho de Monte (site MM), a night roost of *c*.100 White-collared Swifts was observed in April 2013 and April 2014 but, despite a thorough search of the canyon interior, no White-collared Swift nests were found.

Discussion

The discovery of the three nests of Spot-fronted Swifts reported here provides the first documented record of the species' occurrence in Panama (G. Angehr, Panama Bird Records Committee, pers. comm.). The distinctive white facial markings of Spot-fronted Swifts were photographed (Figs. 2–3). This little-known species has been reported nesting at 1,900 m elevation in central Costa Rica (Marín & Stiles 1992), 1,900 m on the west slope of the Andes in Ecuador (Marín & Stiles 1993), 2,050 m on the east slope of the Andes in Ecuador (Greeney 2004), 1,100 m in the central Costal Cordillera of northern Venezuela (Collins 1980) and at 1,745–1,945 m in western Panama (this study). Spot-fronted Swift has

also been observed in Colombia (Chávez-Portilla *et al.* 2007) at 1,800 m. It is notable that we found three pairs nesting close to each other along just one tributary of the Caldera River, and not elsewhere in Chiriquí province, despite searches of other waterfalls. More surveys are required to clarify the species' distribution, but present data indicate that Spot-fronted Swift nests at montane waterfalls at 1,100–2,050 m elevation and is rare and local with a disjunct range.

This study also yielded the first report of nesting White-chinned Swifts (Figs. 5–7) in Panama. Although White-chinned Swift is widely distributed, with records from Belize to Peru, there are few published reports of nesting: in Costa Rica at 700 m elevation (Sardinal River: Stiles & Skutch 1989) and 1,900 m (Tiribí River: Marín & Stiles 1992), in Amazonas, Brazil (Whittaker & Whittaker 2008) at 100 m, in Acre, Brazil (Biancalana & Magalhães in press) at 286 m, and in eastern Venezuela (Ayarzagüena 1984) at 860 m. In Surinam, the species is suspected of nesting at *c*.500 m (Ottema 2002). In Panama, we found them nesting at sites ranging from 880 m to 1,980 m. The two previous records from Panama (Wetmore 1968) are both of specimens: one taken in San Blas province in July 1932, and one on Coiba Island in March 1957. The lack of subsequent sight records in Panama may reflect the difficulty of identifying this species in flight. The data presented here indicate that White-chinned Swift nests at 100–1,980 m elevation, and is uncommon but not rare near mountain waterfalls in Chiriquí province, Panama.

Because both White-chinned Swifts and Black Swifts have dark, unpatterned plumage and subtle facial markings, field separation of these two species at the nest is not straightforward, and we were initially unsure which species was involved in our observations. Marín & Sánchez (1998) reported Black Swifts nesting along the Tiribí River, Costa Rica, 300 km from our study area; White-chinned Swift also nests at this locality (Marín & Stiles 1992). To resolve identification, we captured an adult swift at site QW and found that its wing and tail measurements were within the range of White-chinned, but smaller than Black Swift (Marín & Stiles 1992). In addition, the trapped swift was in wing moult. Black Swifts breeding in North America are not known to moult their flight feathers during the breeding season (Pyle 1997), whereas White-chinned Swifts moult during the nesting season in Costa Rica (Marín & Stiles 1992). The original species description by Zimmer (1945) indicates that a diagnostic feature of White-chinned Swift is that the pale markings on the top of the head are restricted to the sides of the forehead. Both adult White-chinned Swifts at the QW nest displayed a small amount of white below the bill and some whitish fringes to the feathers on the side of the forehead (Fig. 4). The other six presumed White-chinned Swifts that we saw at nests possessed a similar face pattern (Figs. 5–7). Black Swifts nesting in North America vary in the amount of white feather fringes on the lores, superciliary area and forehead (C. Gunn pers. comm.) and, in particular, adults can show pale dusky fringes to the chin and crown. It appears from our observations that adult White-chinned Swifts in Panama lack pale feather fringes to the centre of forehead and crown, which can often be seen in adult Black Swifts, and that White-chinned Swifts can have markedly white chins, unlike the dusky chins sometimes observed in Black Swifts.

An additional morphological feature that has been noted as a difference between Whitechinned and Black Swifts is the presence of an exposed rachis projecting from the tips of the rectrices in *C. cryptus*, which is absent in *C. niger* (Marín & Stiles 1992, Pyle 1997) except on worn rectrices (C. Gunn pers. comm.). The heavily worn tail of the swift we trapped shows that while this may be a useful character for fresh and unworn rectrices, it is not useful for identification during the nesting season, when adult White-chinned Swifts have worn tails. Nostril shape has also been demonstrated to separate these species (Zimmer 1945, Marín & Stiles 1992), with Black Swifts possessing elliptical nostrils and White-chinned



Figure 6. Adult White-chinned Swift *Cypseloides cryptus* incubating, site L3, western Panama, 30 May 2014 (Lloyd Cripe)

Figure 7. Adult White-chinned Swift *Cypseloides cryptus* incubating or brooding, site MM, western Panama, 19 June 2014 (Eric G. Horvath)

Figure 8. Probable White-chinned Swift *Cypseloides cryptus*, 20 km from known nest sites, Chiriquí River, western Panama, 15 April 2014; at least one photographed within a flock of Chestnut-collared Swifts *Streptoprocne rutila* foraging low over riparian canopy trees. Note white chin and white scaling on belly that eliminates Chestnut-collared Swift. Compared to Black Swift *Cypseloides niger*, White-chinned Swift has relatively shorter wings, but this field mark varies considerably in both species, depending on whether they are gliding or stalling, and should not be considered diagnostic (Eric G. Horvath)

Swifts having more rounded nostrils. We were unable to evaluate this character in the field, despite using high-quality telescopes, because the nostrils are so small and field conditions precluded close approach to nests.

Shape in flight has been noted as another means to separate Black Swifts from Whitechinned Swifts by Howell & Webb (1995), who emphasised the cleft tail (diagnostic) and relatively longer tail and wings of Black Swifts. However, Pyle (1997) demonstrated that only older male Black Swifts display a notched tail; the tail is square-ended in females and first-years of both sexes. Photographs of Blacks Swifts in flight at nesting areas in North America (EGH unpubl.) indicate that wing shape varies substantially between slender and sickle-shaped to broader. For separating White-chinned from Black Swifts, we found flight shape useful only with the aid of good photographs and, in the case of swifts lacking a forked tail, we consider shape alone to be an unreliable means of specific identification for most observations of *Cypseloides* in flight, particularly at localities where three *Cypseloides* species occur.

Chestnut-collared Swift is readily identified in the field under good lighting by their broad chestnut collar and upper breast-band, a feature shown by all males. Females also possess a bright collar, but often it is 'abbreviated' dorsally or absent there (Stiles & Skutch 1989, Howell & Webb 1995). There are many sight records in Panama, but breeding distribution is poorly known. As we found nests at widely scattered locations and at highly variable elevations, we suggest that Chestnut-collared Swift is probably a commoner nesting bird in western Panama than previously recognised.

Our data on nesting phenology of Spot-fronted, White-chinned and Chestnut-collared Swifts in Panama reveal a pattern of nest initiation in late April, egg laying in May (following the start of the wet season) and fledging in late July / August. In Costa Rica, Marín & Stiles (1992) found that these three species all breed at the same time of year, from the start of the rainy season and continuing from May into August. In Venezuela, Collins (1980) observed a Spot-fronted Swift nest with eggs in mid July. The length of the nestling period for Spot-fronted Swifts observed in our study was *c.*60 days, similar to the 65 days reported by Marín (2008). In contrast, White-collared Swifts appear to start nesting at the end of the dry season, *c.*1 month earlier, as we observed large young in the nest in June. This places egg laying in early April for Panama, matching *S. zonaris* phenology in Costa Rica (Marín & Stiles 1992).

The Cypseloidine swift habit of nesting at shaded, cool and humid cliffs near or behind waterfalls is well known (Knorr 1961, Collins 1968, Marín & Stiles 1992, Levad *et al.* 2008), and probably has adaptive significance. Three hypotheses, which are not mutually exclusive, have been proposed regarding the selective advantage of waterfall nesting.

The first hypothesis relates possible torpor to nest site location. Torpor in Black Swifts was proposed by Udvardy (1954) who extrapolated from the Koskimies (1948) torpor study of Common Swift Apus apus. While the adults are away from the nest, the nestling may survive the period of cold by temporarily becoming torpid; by reducing body temperature the loss of body weight from starvation is diminished. Boyle (1998) linked possible torpor and nest ambient temperature by hypothesising that the constantly cool temperatures would aid in slowing the metabolism of the Black Swift nestling when it was alone. Air temperature at Black Swift nests has been documented to be especially stable, varying little (Gunn et al. 2012). Foerster (1987) observed that older Black Swift nestlings are typically left unattended for long periods during the day, which could suggest possible use of torpor. At dusk adult Black Swifts return to the nest and brood the chick, making torpor unnecessary at night. Field observers have searched for torpor-like behaviour in adult and nestling Black Swifts, but torpor has not been observed (Legg 1956, Gunn et al. 2012). Although there is an absence of experimental or behavioural studies demonstrating torpor in Cypseloidine swifts, they may possess this capacity. While torpor cannot be eliminated, to date no studies have demonstrated its regular use.

A second hypothesis, developed by Marín & Stiles (1992), relates high humidity to nest stability and adhesion to the cliff. *Cypseloides* construct their nests on ledges or niches in vertical cliffs, and sometimes these ledges are precariously small. For Black, White-chinned and Spot-fronted Swifts, nests are often constructed of live mosses that 'root' to the cliff with their anchoring rhizoids, enhancing nest stability on insecure ledges. The high humidity found near and behind waterfalls permits the mosses that form the nest cup to continue growing after having been plucked from the cliff during nestbuilding. Nests composed of mosses rooted to the cliff are more secure and less apt to fall. In coastal areas, Black Swift nests were found to be constructed of seaweed (Legg 1956), so rooting by mosses is not a requirement at all localities. For White-collared Swift, often the egg is simply laid on a rock ledge with little or no nest material (Marín & Stiles 1992). Overall, the nest adhesion hypothesis can be seen as an additional supporting factor but not explanatory for all Cypseloidine waterfall nesting situations.

The third hypothesis is avoidance of predation. It has been proposed that Black Swift nests are associated with waterfalls to limit predator access (Knorr 1961, Marín & Stiles 1992, Levad *et al.* 2008). Nest success for most small, open-nest birds is 40–60% (Ricklefs 1969) even though they have short nesting cycles of 25–30 days. However, among the four species of Cypseloidine swifts studied by Marín & Stiles (1992) in Costa Rica, nest success rates averaged 71%, despite the long nesting cycle of 80–90 days. Data from our study in Panama suggests that nest success among Spot-fronted Swifts may be relatively high, although our sample size is tiny (n = 3). The most comprehensive study of Black Swifts, in Colorado, USA, revealed a nest success rate of 72% (Hirshman *et al.* 2007). The low reproductive rate of Cypseloidine swifts, with clutches of either two eggs in *Streptoprocne* or one in *Cypseloides* (Marín & Stiles 1992), combined with the long nesting cycle, strongly suggests that all require extraordinarily safe places to nest.

We propose that waterfall nesting locations provide uniquely high levels of safety from predation for the following reasons. First, snakes and small mammals (i.e. rodents and procyonids) that routinely climb dry, vertical rock faces cannot scale the slippery algae and moss on the vertical, permanently wet cliffs at waterfalls. Second, waterfalls are loud and mask sounds at the nest. Third, the strong moist winds generated by waterfalls may disperse nest odours. Finally, Cypseloidine swifts often nest behind the 'veil' of falling water and these dripping locations help to visually conceal the nests from avian nest predators such as corvids and raptors. We predict that experimental studies of nest predation that compare waterfall locations to dry-cliff sites not associated with waterfalls will demonstrate lower predation rates at waterfall nesting locations.

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